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The effects of substrate and shell form on burrowing in the Genus *Katelysia* (Bivalvia:Veneridae)

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ABSTRACT

The genus *Katelysia* in Southern Australia is represented by three species with distinctive but variable shell forms. These range from narrow shells with marked concentric sculpturing to obese shells with little sculpturing. Comparative investigation of the burrowing process of the three species and a possible sub-species of one, revealed that, in general, *K. scalarina* was the most and *K. peroni* the least efficient in all phases of burrowing. A theoretical consideration is made of shell characteristics believed to influence burrowing in an attempt to account for the different burrowing efficiencies of the different forms.

INTRODUCTION

The genus *Katelysia* (Bivalvia:Veneridae) is somewhat problematic in Southern Australia in that the three currently recognized species viz. *Katelysia scalarina* (Lamarck, 1818), *Katelysia rhytiphora* (Lamy, 1935) and *Katelysia peroni* (Lamarck, 1818) show such a wide range of intraspecific variation that specific identification can sometime be difficult. In addition, certain localized populations in South Western Australia are so characteristic as to have induced sub-specific recognition (*Katelysia scalarina polita* Nielsen, 1963). During an investigation into this systematic problem, I felt that an experimental investigation of the burrowing of different shell forms would be a useful adjunct to the more traditional approaches of shell morphometry and studies of reproductive cycles; these, together with electrophoretic investigations will form the basis of a more detailed subsequent publication on the subject.

Early studies of bivalve burrowing were observational and descriptive and, until the work of Ansell (1962) on selected Veneridae, did not involve continuous recording of the process. The use of electronic and cinematographic techniques, as well as kymograph recordings in the sixties, marked a period of increased interest in invertebrate locomotion in general and bivalve burrowing in particular. These investigations resulted in a fairly thorough understanding of the mechanics of bivalve burrowing and culminated in reviews by Trueman (1968) and Trueman and Ansell (1969) and the important contributions of Stanley (1970).

Although the family Veneridae includes a wide range of shell forms and was one of the first groups in which burrowing was investigated in detail, there have been few attempts to relate shell form and substrate within this family.

The use of the terms 'mud cockle' to indicate a preferred habitat of *K. peroni,* an obese form with minimal shell sculpture and 'sand cockle' for the well sculptured, narrow *K. scalarina,* by Cotton (1961), suggested to the author that the problem might be fairly straightforward with forms such as *K. peroni* ideally suited to fine sediments and the more highly sculptured forms suited to coarse sediments. However, as details emerged during the investigation it became apparent that shell characters are by no means easily related to burrowing ability.

MATERIALS AND METHODS

In order to avoid difficulties of interpretation, which might arise from investigating too wide a range of shell forms, only four of the most distinctive shell forms were used in burrowing experiments. For similar reasons, only the four sediments of origin of the selected shell forms were used for experimentation. Shell forms included *K. scalarina* from Princess Royal Harbour, Albany, *K. scalarina* from Seine Bay, Augusta (= *K. scalarina polita* of Nielsen, 1963), *K. rhytiphora* from Oyster Harbour (Site 1), Albany and *K. peroni* from Oyster Harbour (Site 2) Albany; collecting sites are shown in Fig. 1. Five individuals of each form were allowed to burrow into each of the four sediments in used 500g margarine containers. In each container approximately 4 cm of sediment was covered with a similar depth of seawater at a temperature of +14°C and +31‰ salinity. Experimental animals were selected within as narrow a size range as feasible.

The burrowing process was timed in two phases. Time intervals were recorded firstly, from initial pedal probing to the point at which the shell had been manoeuvred into an upright position and secondly, from this stage to the point at which the animal was just covered by the sediment. Since no continuous recording equipment was used subsequent locomotory activities could not be followed. However, *Katelysia* has short siphons so that burrowing is likely to stop soon after the animal is covered. The number of burrowing sequences was not recorded. After experimentation, the following parameters were recorded for each individual: 1) Length (L); 2) Height (H); 3) Width (W) (Fig. 2) and 4) Dry Shell Mass (M).

From the results obtained the following values were calculated for each individual:

1) Uprighting Rate Index (U.R.I.) $= \sqrt[3]{\dfrac{\text{Shell Mass (g)}}{\text{Uprighting time (secs)}}} \times 100$

2) Burrowing Rate Index (B.R.I.) $= \sqrt[3]{\dfrac{\text{Shell Mass (g)}}{\text{Burrowing time (secs)}}} \times 100$ (Stanley, 1970)

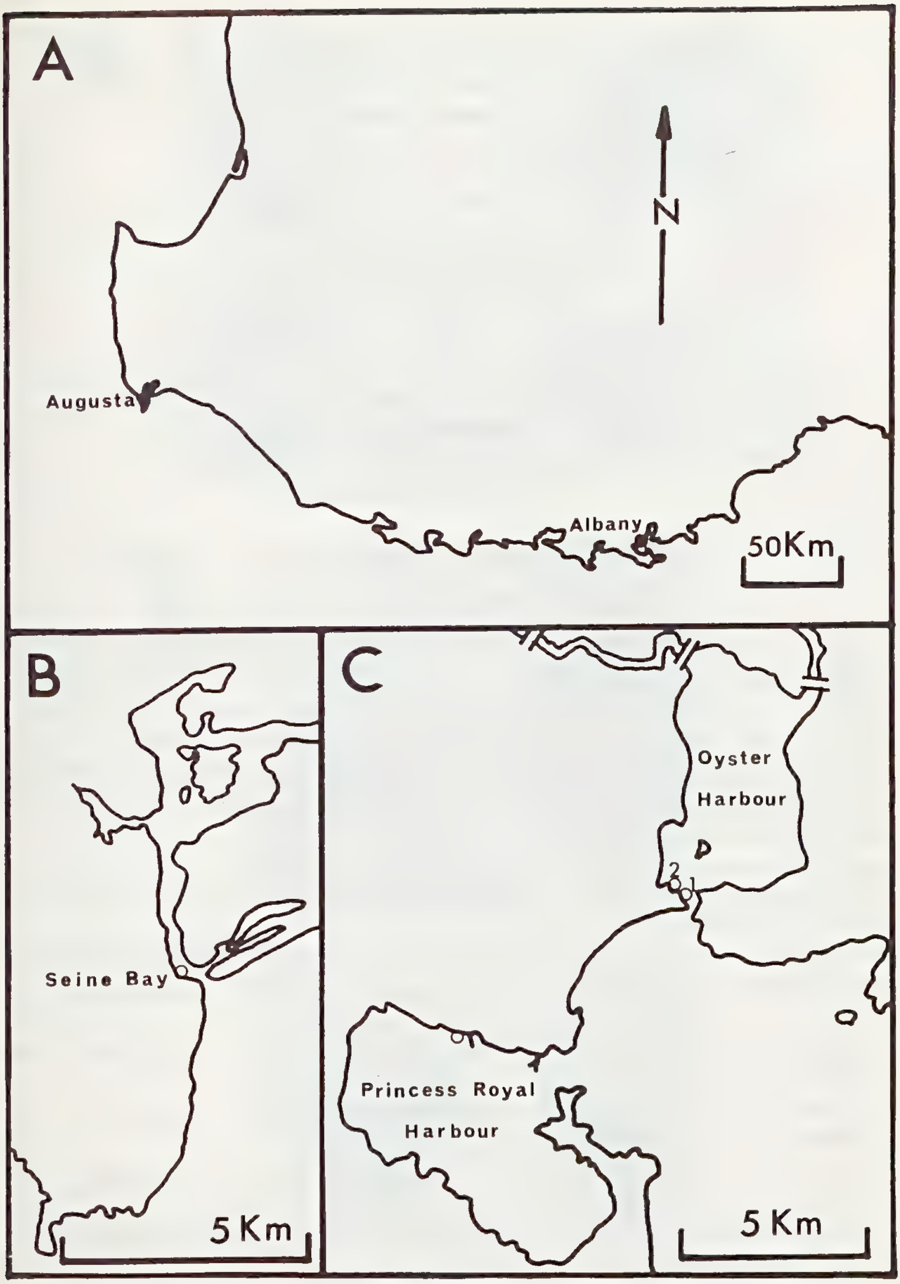
3) Index for Combined (Uprighting plus Burrowing) Times (C.R.I.)

$$= \sqrt[3]{\frac{\text{Shell Mass (g)}}{\text{Uprighting + Burrowing time (secs)}}} \times 100$$

The second formula is taken directly from Stanley (1970) and the other formulae are obvious simple modifications of this. Individual values were averaged to give three rate indices for each form in each sediment (U.R.I., B.R.I. and C.R.I.). Shell measurement were expressed in terms of W/H (shell obesity) and M/L (shell density) ratios as the most useful estimates of shell character pertinent to burrowing. No quantitative measure of shell sculpture was taken.

Sediment characteristics were determined after oven drying, by sieving through a graded series of sieves on an automative shaker and weighing the contents of each sieve. The weights were plotted on a cumulative percentage basis and the median particle size estimated from the resultant curve.

In addition to the quantitative recordings described above, features generally observed for different shell forms as they burrowed were also noted.



1. Map showing sites from which experimental animals were obtained. A) General locality map of S.W. Australia with enlarged insets of B) Augusta Area (34°22'S 115°10'E) and C) Albany area (34°58'S 117°57E)

2. Measurements used to estimate different shell characters. For key see text.

RESULTS

The different shell characters of the experimental animals are clearly illustrated in Fig. 3 and Table 1. Both *K. scalarina* (Augusta) and *K. peroni* tend to be obese and smooth or weakly sculputured while *K. scalarina* (Albany) is narrow in profile with angular concentric ridges. *K. rhytiphora* is also narrow in profile with rounded concentric ridges and fine radial striations. Quantitative estimates of shell characters (Table 1) show the following sequences of a) increasing obesity (W/H): *K. rhytiphora, K. scalarina* (Albany) *K. scalarina* (Augusta) and *K. peroni;* b) increasing shell density (M/L): *K. rhytiphora, K. scalarina* (Albany), *K. peroni, K. scalarina* (Augusta). The only difference between these is the relative positions of *K. peroni* and *K. scalarina* (Augusta).

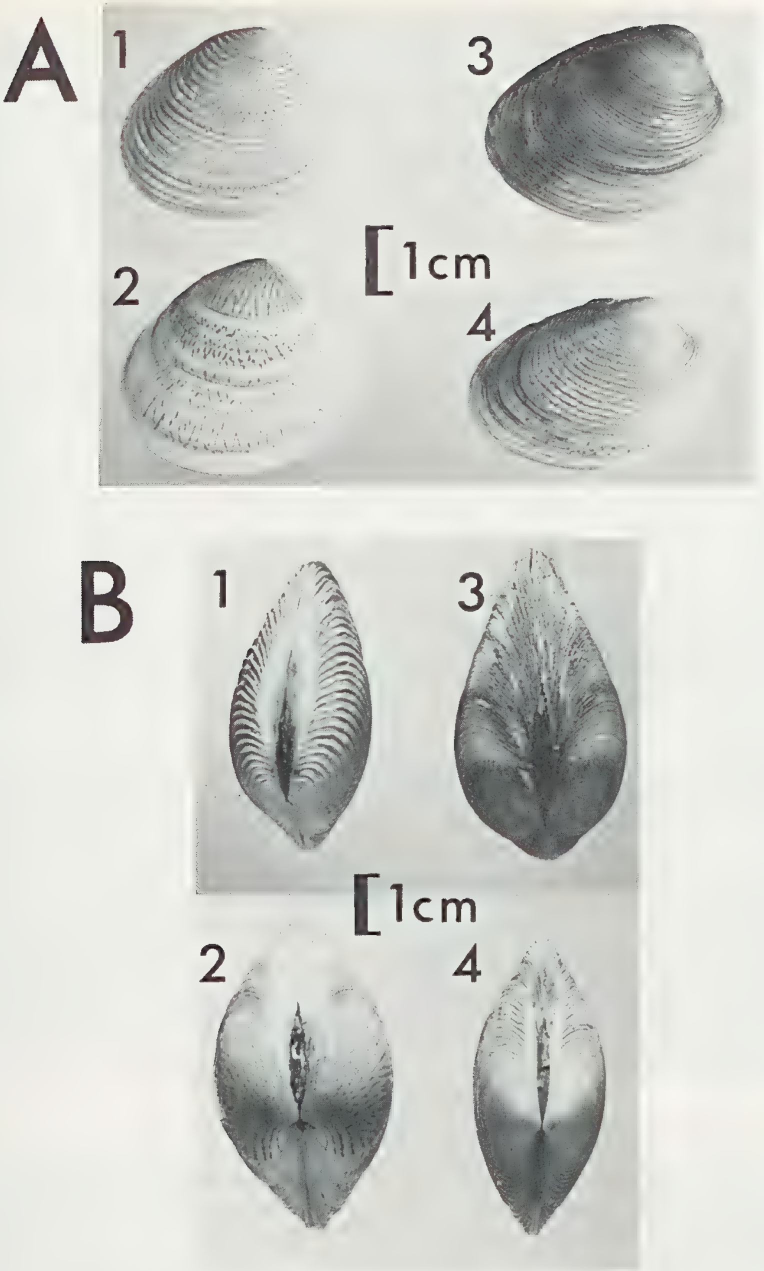
Table 1. Numerical values for two shell characteristics for different forms of *Katelysia*. Standard deviations are given after each value and the number of animals used in each case is in parentheses.

Shell Form	Source	Shell Obesity	(W/H)	Shell Density	(M/L)
K. rhytiphora	Oyster Harbour, Site 1	0.54 + 0.34	(14)	1.14 + 0.161	(14)
K. scalarina (Albany)	Princess Royal Harbour	0.56 + 0.215	(20)	1.29 + 0.335	(20)
K. scalarina (Augusta)	Seine Bay, Augusta	0.59 + 0.022	(20	1.99 + 0.259	(20)
K. peroni	Oyster Harbour, Site 2	0.64 + 0.058	(17)	1.53 + 0.363	(17)

Table 2. Rate Indices for different Katelysia shell forms burrowing in different sediments)

a) Uprighting Rate Indices (U.R.I.'s)

Source	Sediment M.P.S. (um)	*K. scalarina* (Albany)	*K. scalarina* (Augusta)	*K. rhytiphora* (O.H.1)	*K. peroni* (O.H.2)
Augusta	98	1.31 (4)	*1.01* (5)	*† 1.48 (4)	0.54 (2)
O.H.1	103	0.83 (5)	*† 1.32 (4)	*0.89* (4)	0.38 (5)



3. External appearance of *Katelysia* shells in: A) Lateral View and B) Dorsal View. 1) *K. scalarina* (Albany); 2) *K. scalarina* (Augusta); 3) *K. peroni;* 4) *K. rhytiphora.*

O.H.2	126	*† 1.46	(5)	0.85	(5)	0.71	(3)	† *0.56*	(4)
P.R.H.	130	**0.975*		0.83	(2)	0.41	(2)	0.40	(3)

b) Burrowing Rate Indices (B.R.I.'s)

Sediment Source	M.P.S. (um)	*K. scalarina* (Albany)		*K. scalarina* (Augusta)		*K. rhytiphora* (O.H.1)		*K. peroni* (O.H.2)	
Augusta	98	* 0.31	(4)	*0.27*	(5)	† 0.22	(4)	0.12	(2)
O.H.1	103	* 0.38	(5)	0.19	(4)	*0.14*	(4)	0.19	(5)
O.H.2	126	* 0.29	(5)	† 0.28	(5)	0.19	(3)	† *0.22*	(4)
P.R.H.	130	*† *0.54*	(5)	0.20	(2)	0.13	(2)	0.19	(3)

c) Indices for Combined (Uprighting plus Burrowing) times (C.R.I.'s)

Sediment Source	M.P.S. (um)	*K. scalarina* (Albany)		*K. scalarina* (Augusta)		*K. rhytiphora* (O.H.1)		*K. peroni* (O.H.2)	
Augusta	98	* 0.22	(4)	† *0.20*	(5)	† 0.19	(4)	0.09	(2)
O.H.1	103	* 0.25	(5)	0.16	(4)	*0.12*	(4)	0.12	(5)
O.H.2	126	* 0.23	(5)	† 0.20	(5)	0.15	(3)	*0.13*	(4)
P.R.H.	130	*† *0.33*	(5)	0.16	(2)	0.10	(2)	† 0.16	(3)

Key: M.P.S. Median particle size; P.R.H. Princess Royal Harbour; O.H.1 Oyster Harbour 1 (Fig. 1); O.H.2 Oyster Harbour 2 (Fig. 1). The values for the sediment of origin are italicized, the highest value for each sediment marked *, and the highest values for each form marked †. Mean values are given and the numbers of animals used in each case is in parentheses.

Table 2 shows the median particle sizes of experimental sediments and rate indices for each species in these sediments. The sediment from Augusta is the least coarse and that from Princess Royal Harbour the most coarse. The sediment from Oyster Harbour site 1 is fairly similar to Augusta sediment while that from Oyster Harbour site 2 is similar to Princess Royal Harbour sediment. *K. scalarina* from Albany has the highest rate indices in all except two cases, i.e. U.R.I.'s in sediments from Augusta and Oyster Harbour, site 1. In these cases *K. rhytiphora* and *K. scalarina* (Augusta) have the highest values in Augusta and Oyster Harbour site 1 sediments respectively. The second highest values throughout are for *K. scalarina* from Augusta, the only exception being the U.R.I. for its sediment of origin. *K. peroni* generally has the lowest rates throughout except for B.R.I.'s which are lowest for *K. rhytiphora* in all sediments other than that from Augusta. The fastest rates for each form are predominantly in the sediment of origin or in a less coarse sediment. In only 3 cases are the rate indices higher for a more coarse sediment than the sediment of origin.

DISCUSSION

The process of burrowing in bivalves is described in detail by Trueman, Brand and Davis (1966a). Theoretical consideration of the factors relating shell form to burrowing characteristics and sediments is made in Trueman, Brand and Davis (1966b) and Stanley (1970, 1975). As a general rule soft, fine sediments are so easy to penetrate that there is a tendency for shelled organisms to sink into them. The most obvious way in which bivalves have overcome this problem may be seen in species such as *Glossus humanus* (L.) in which the shell is lightweight and obese (Owen, 1953). In contrast to fine sediments, coarse substrata are difficult to penetrate. Bivalves have overcome the problem of burrowing into such sediments by evolving a well developed foot for active pedal probing (*G. humanus* by contrast has a poorly developed foot, Owen, 1953) and shell ornamentation (as a frictional aid).

The results of the experiments reported here can, with some exceptions, be interpreted in the light of the theoretical considerations outlined above. The importance of shell sculpture in the intial phase of shell uprighting became very apparent when making comparative observations of *K. scalarina* from Albany and *K. peroni* on coarse sediments which become hard due to rapid compaction. In *K. scalarina* (Albany) initial uprighting was achieved rapidly as the concentric ridges acted as a brake against shell displacement during pedal probing. The ridges in *K. scalarina* (Albany) are triangular in section which would enhance this effect. By contrast, the shell of *K. peroni*, which has reduced sculpturing and little substrate contact because of its obesity, rotated during pedal probing on coarse substrata; it was only with some difficulty that uprighting was achieved in this species.

The B.R.I.'s (Table 2b) fall between 0.1 and 0.5, Stanley's (1970) range for slow burrowers. *K. scalarina* (Albany) has the highest B.R.I. values for each sediment and *K. rhytiphora* the lowest for all except Augusta sediment in which *K. peroni* was the slowest burrower. The comparatively high rates of *K. scalarina* (Albany) are again, I believe, related to both shell shape and sculpturing. Its narrow shell section aids sediment penetration while the concentric ridges, although according to Stanley's interpretation (1970) offering a resistance to penetration, probably facilitate burrowing by acting as an efficient penetration anchor and to some extent by lifting sediment during shell rocking. The comparatively high B.R.I.'s for *K. scalarina* (Augusta) may be explained in terms of its high shell density, which would overcome the problem of its higher obesity, whereas the shell of *K. peroni* has a lower shell density so that problems associated with its high obesity would not be affected. The low B.R.I.'s for *K. rhytiphora* reflect a tendency for this species to plough through rather than burrow into the sediment. This behavioural feature was also noted in the field but the author cannot suggest a reason for this trait in a suspension feeding bivalve. Although *K. rhytiphora* was not examined for parasites in this study, erratic burrowing has been noted (personal observations) in heavily parasitized European Venerids of the genus *Venerupis*.

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In theory, increasing obesity would tend to reduce uprighting and burrowing efficiency while increasing shell density would tend to oppose this. The data presented above proved difficult to interpret, not only because of these opposing factors but also as a result of the influence of shell sculpture, which was not quantified. Although somewhat simplistic, the attempt to relate these factors goes some way towards an understanding of the problem but it should not be overlooked that the ultimate form of the shell of a burrowing bivalve is a compromise between several factors (Eagar, 1978) not all of which have been assessed here.

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